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Conservation Assessment for the American Marten in the Black Hills National Forest, South Dakota and Wyoming

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INTRODUCTION

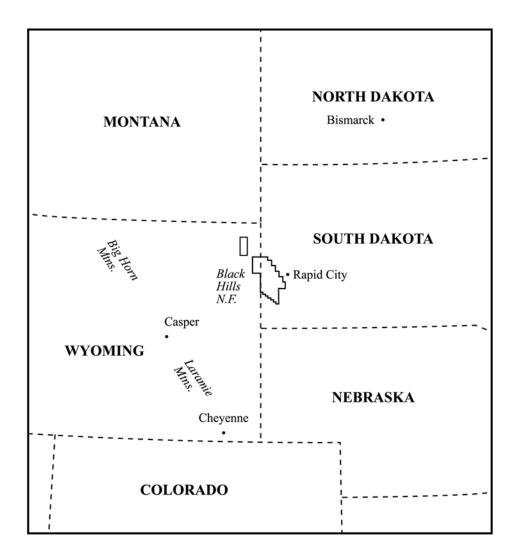
This report assesses the biology and overall conservation status of the American marten (*Martes americana*) in the Black Hills National Forest of South Dakota and Wyoming. It describes and evaluates the status of martens and the state of knowledge about the species in the Black Hills National Forest and adjacent areas (Figure 1). It evaluates the scientific basis for assessing the distribution and abundance of martens in the Black Hills and surrounding areas, and for managing and monitoring martens and the habitats likely to be important to them. An assumption of this assessment is that viability of the marten population in the Black Hills is a goal of management, and that viability of martens is defined in terms of probability of population persistence over specified periods, typically centuries.

This assessment is based on scientific knowledge, meaning that it relies primarily on the peer-reviewed scientific literature. Other sources, including unpublished reports, manuscripts in review, unpublished data in agency files and personal communications, are used where peer-reviewed publications do not treat a particular subject adequately. However, these unpublished accounts are clearly identified, and are considered to be a less reliable form of knowledge than peer-reviewed published accounts. For the purpose of this assessment, master's theses and doctoral dissertations are considered to be publications, although I recognize that they have not undergone anonymous peer review.

In almost all subject areas, the only scientific knowledge about marten ecology or conservation derives from outside the Black Hills. Therefore, I extrapolate from other areas where martens have been studied to the Black Hills, assuming the general similarity of marten response to environmental conditions in the Black Hills and elsewhere. I emphasize study areas, for example the Rocky Mountains, over other regions, for example the Northeast. Because of the extent to which I extrapolate to the Black Hills from marten studies conducted elsewhere, I provide extensive qualification of such extrapolations, so that the reader can assess the likelihood that this geographic extrapolation will lead to correct conclusions about martens in the Black Hills.

A further assumption of this assessment is that the principles that have been advanced for the conservation of low-density, environmentally sensitive species in the face of scientific uncertainty are validly applied to the marten in the Black Hills. Ruggiero and McKelvey (2000) summarized these principles for the lynx (*Lynx canadensis*), and the Interagency Grizzly Bear Committee (1999, unpublished) for the grizzly bear (*Ursus arctos*). These principles partially embrace those of the precautionary principle (Raffensperger and Tickner 1999), which states in part that uncertainty and risk should be acknowledged openly and quantified where possible, that uncertainty should be expressed in the form of competing hypotheses, and that limitations of databases and known or likely biases in knowledge should be clearly acknowledged. The precautionary principle further proposes that inferences and speculations should be clearly identified, and they are so identified here.

Figure 1. Location map of the Black Hills National Forest and surrounding areas.



Areas Of Uncertainty

Ecological knowledge about martens specific to the Black Hills is very limited. No peer-reviewed scientific publications dealing explicitly with distribution, population ecology, habitat ecology, diet, behavior, population genetics or movements of martens in the Black Hills had been published as of April 2000. The reason for this is simple: martens were scarce or absent in the Black Hills for much of the 20th century; they have been present in numbers sufficient to permit ecological study only for about 10 years, having gone extinct in mid-century and been reintroduced in the 1980's and 1990's (Fredrickson 1989, unpublished report), and field studies currently underway (e.g. Fecske et al., in review) will be the first to report on habitats and movements of martens in the Black Hills. Therefore, a high degree of uncertainty accompanies many or most of the inferences and predictions in this assessment.

CURRENT MANAGEMENT SITUATION

Management Status

The current management status of the American marten in the U.S. and Canada is shown in Table 1. Neither the American marten nor any of its local populations are listed under the Endangered Species Act. Likewise, as of 1 September 2000, the species had not been listed in appendices to the Convention on International Trade in Endangered Species of Wild Flora and Fauna, or in the World Conservation Union Red Book. The marten on Newfoundland Island (an endemic subspecies, *M. americana atrata*) has been classified as threatened since 1986 (Forsey et al. 1995). The marten on Cape Breton Island, Nova Scotia is being considered for provincial or federal listing as of fall 2000.

In six western state jurisdictions (California, Colorado, Nevada, New Mexico, South Dakota, and Utah), martens cannot be legally taken in any part of the jurisdiction at any time, an increase of one state since 1994. California classifies the marten as a furbearer, but has had no open season since 1952. In Colorado, trapping, the only legal means of taking martens, was banned by referendum in 1996 (Andelt et al. 1999). Vermont classifies the marten as a furbearer, but has no open season. Only six other states give the marten formal conservation protection: "protected" in Utah and Nevada, "Endangered, Group II" in New Mexico, "endangered" in Wisconsin, and "threatened" in New Hampshire. The meanings of these classifications are specific to the jurisdiction. In South Dakota, where the Black Hills population is largely found, the marten is protected by state regulation. Where martens occur in the Wyoming portion of the Black Hills, they can be legally trapped at the discretion of the game warden with responsibility for the area.

Aside from protective restrictions, several U.S. and Canadian land management agencies assign special planning significance to the marten. Pursuant to the National Forest Management Act of 1976 and 36 CFR Ch. II, Part 219.19 a. 1., many forest plans in Regions 1, 2, 4, 5, and 6 of the National Forest System have designated the marten as an ecological indicator species (e.g., Gallatin National Forest) or a "high-interest species" (e.g., Wasatch-Cache National Forest). These designations were summarized by Macfarlane (1994). Further, Regions 2 and 5 have designated the marten as a "sensitive species," one for which population viability is a concern, as evidenced by a current or predicted downward trend in population numbers or habitat (Forest Service Manual 2670.5).

Table 1. Management status of the American marten in United States and Canada as of September 2000.

Jurisdiction	Status	
United States		
Idaho	Furbearer	
Montana	Furbearer	
Colorado	Furbearer, trapping of any species prohibited	
Alaska	Furbearer	
California	Furbearer, closed season	
Idaho	Furbearer	
Maine	Furbearer	
Massachusetts	Extirpated	
Minnesota	Furbearer	
Nevada	Protected (NRS 501)	
New Hampshire	Threatened (under State classification)	
New Mexico	Endangered, Group II	
Oregon	Furbearer (vulnerable)	
South Dakota	Protected	
Utah	Protected	
Vermont	Furbearer, no open season	
Washington	Furbearer	
West Virginia	Extinct	
Wisconsin	Endangered (under State classification)	
Wyoming	Furbearer	
Canada		
Alberta	Furbearer	
British Columbia	Furbearer	
Manitoba	Furbearer	
Newfoundland	Furbearer, closed season, federally threatened	
Northwest Territories	Furbearer	
Nova Scotia	Furbearer, closed season, species of concern on Cape Breton Island, expected to be listed as endangered	
Ontario	Furbearer, special management species	
Prince Edward Island	Extinct	
Quebec	Furbearer, indicator species	
Saskatchewan	Furbearer	
Yukon	Furbearer	

Existing Management Plans, Assessments, Or Conservation Strategies

The following are species assessments, management plans, or conservation strategies for the American marten (please see Literature Cited for full citations):

Bennett and Samson 1984a; Beaudette 1991; Biological Staff 1996; Forsey et al. 1995; Marshall 1994; Patton and Escano 1990; Rodrick and Milner (eds.) 1991; Ruggiero et al. 1994; Watt et al. 1996.

Boggs (1995, http://www.wildrockies.org/ActivOrg/PredProj/Ppnews/Fall_95/ PP_fores.html) reported that of 20 national forests in the Rocky Mountains (Beaverhead, Bighorn, Bitterroot, Boise, Bridger-Teton, Caribou, Clearwater, Colville, Custer, Deerlodge, Deschutes, Flathead, Fremont, Gallatin, Gifford Pinchot, Helena, Idaho Panhandle, Kootenai, Lewis and Clark, Lolo) that were surveyed by the Predator Project, none had implemented approved conservation strategies for forest carnivores (marten, fisher [*M. pennanti*], lynx and wolverine [*Gulo luscus*]) collectively or for individual species.

REVIEW OF TECHNICAL KNOWLEDGE

Systematics

Most systematic studies of martens have been based on morphology; only two studies (Carr and Hicks 1997, Stone 2000) based on molecular markers have been completed. In the first half of the 20th century, the American marten was classified as from two (Merriam 1890) to six species (Miller 1924), but was unified to a single species by the mid-1900's (Hall 1981). Up to 14 subspecies have been recognized (Hall 1981), but Hagmeier (1958, 1961) and Anderson (1970) considered these distinctions arbitrary, and Clark et al. (1987) recognized only eight subspecies in two "subspecies groups:" "americana" and "caurina." Remarkably, Carr and Hicks (1997), based on mitochondrial DNA markers, proposed two species of American marten, M. americana and M. caurina, corresponding with the subspecies groups. Consistent with this view, the existence of two major taxonomic groups of American martens was supported by analyses of nuclear DNA markers by Stone (2000). However, many ecological questions would have to be answered before two species of American marten would be accepted by the systematics community. The lengthy zone of contact between these putative subspecies groups, or species, runs from Southeast Alaska eastward to the Canadian plains; pre-settlement martens in the Black Hills were in subspecies M. a. caurina using the classification of Anderson (1970), and would be considered *M. caurina* under the classification proposed by Carr and Hicks (1997).

Pre-settlement martens in the Black Hills would be considered *M. a. vulpina* under Hall's (1981) classification, but Hall did not map or recognize any of the insular marten populations east of the Rocky Mountain mainland: in central Montana (Wisz 1999), in the Bighorn Mountains, or in the

Black Hills (Turner 1974). Turner (1974) identified the marten as a "species of uncertain status in the Black Hills region," using *M. a. vulpina*. Some other mammal species on isolated mountain ranges in the Great Plains have received subspecific recognition. These include the snowshoe hare in the Bighorn Mountains (*Lepus americanus seclusus*) and the southern redbacked vole in the Black Hills (*Clethrionomys gapperi brevicaudus*) (Hall 1981). Martens native to the insular Bighorn Mountains and Black Hills have not received such taxonomic designation. Martens reintroduced into the Black Hills from Colorado were *M. a. origenes* (Hall 1981) and from Idaho likely were *M. a. vulpina*, depending on the source location.

Distribution And Abundance

The American marten represents the easternmost extension of the boreal forest martens (also including *M. martes*, *M. zibellina*, and *M. melampus*), which extend across the circumboreal zone. These species were considered a superspecies by Anderson (1970), and exhibit some ecological similarities to American martens (Buskirk 1994). The distribution of the American marten includes moist coniferous forest of boreal and taiga North America and its southern montane extensions, and has been reviewed and updated by Gibilisco (1994). To the north, the marten extends to the northern limit of trees; southward, it extends to the southern Sierra Nevada, to northern New Mexico in the Rocky Mountain mainland, and in the east it extended to Illinois, Ohio, and Pennsylvania in pre-settlement times. American martens occur almost exclusively in areas with cold, snowy winters; snow depth may be important to martens as it confers competitive advantages over some other carnivores (Krohn et al. 1995, 1997) and insulation for winter resting sites (Buskirk et al. 1989). The abundance of martens varies strongly with site and time; no broad generalizations can be drawn.

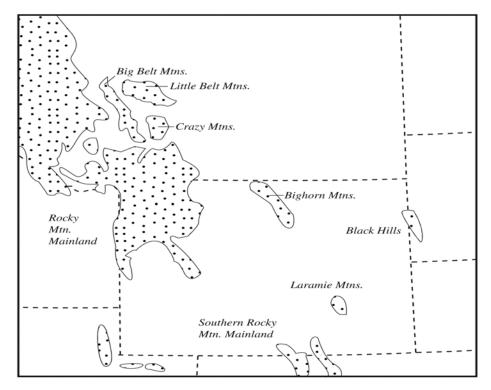
Distribution Recognized In Primary Literature

Of greatest interest relative to the Black Hills is the distribution of martens, and discontinuities in the distribution, in isolated mountain ranges east of the Rocky Mountain mainland, including the Black Hills. This distribution is summarized in Figure 2. Martens are known from the Black Hills in the 19th century (Hoffman 1877), although nothing is known about their pre-settlement distribution within the Black Hills. The Black Hills appear to have lost their native marten population in the mid-1900's, and reintroductions occurred in the 1980's and 1990's; this is the only site of marten reintroductions in or near the Rockies (Berg 1982).

In the Bighorn Mountains of northern Wyoming martens are restricted in distribution but locally common (Beauvais 1997), and their conservation status is uncertain. Beauvais (1997) observed marten tracks on only four of 14 snow transects (37.4 km total length) distributed widely in coniferous forests of the Bighorns. Francis Parkman (1931) described "sables" and "martens" being trapped in the Laramie Mountains of east-central Wyoming in the 1840's, but martens do not occur in the Laramie Mountains today (Luce et al. 1999), and may not have at any time in the 1900's. Other apparently isolated mountain ranges east of the Rocky Mountain mainland that have held native marten populations in historical times include the Big Belt Mountains, the Little Belt Mountains, and the Crazy Mountains. Thus, various mountain ranges east of the Rocky Mountain mainland hold or have held marten populations in historical times (1830 – present). Some of these have lost and others have retained their populations. The Laramie Mountains provide a rough biogeographic parallel to the Black Hills in being isolated from the main distribution of martens in the Rocky Mountains, in having had written records from the 1800's of martens occurring there, and in having apparently lost martens at some time between their

original description and the mid-twentieth century. No specimens of the original, native martens from either mountain range are known.

Figure 2. Pre-settlement distribution of marten populations in the Rocky Mountains and isolated ranges east of the Rockies.



American martens are very dispersal-sensitive, meaning that they are unlikely to move through areas lacking certain habitat traits. Martens are apparently unable to disperse across non-forested areas below timberline wider than about 25 km (Wisz 1999). This is based on the absence of martens from habitat patches apparently large enough to support multiple animals (>400 km²), but separated from forest occupied by martens by as little as 6.5 km of non-forested land below timberline. Wisz (1999) was not able to rule out the possibility that the absence of martens from some isolated patches was due to poor population persistence in those isolated patches, rather than inability of martens to colonize them. In any case, extensive non-forested areas below timberline appear to pose complete barriers to dispersal by martens, with important implications for population insularity in the Black Hills and other isolated mountain ranges. It is unknown whether martens in isolated mountain ranges, including the Black Hills, are simple remnants of a broader and more contiguous Late Pleistocene distribution, the vicariance hypothesis proposed by Brown (1971) for montane mammals of the Great Basin. Alternatively, isolated marten populations such as those in the Black Hills could represent an equilibrium between colonization

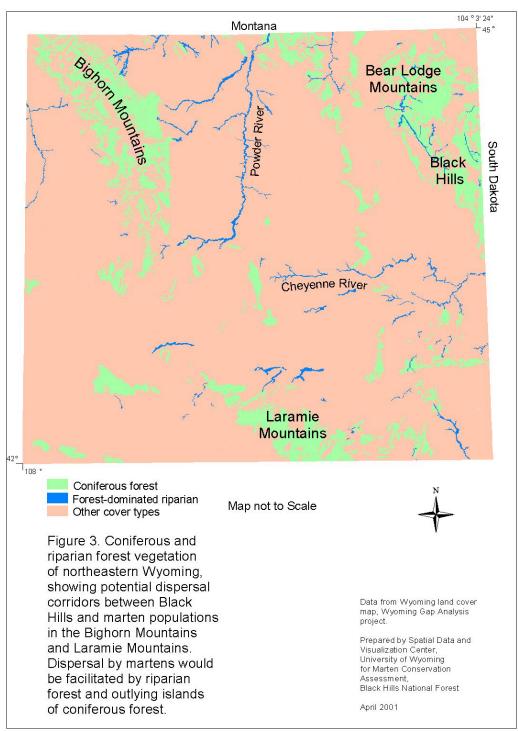
and extinction events in post-glacial times, the equilibrium hypothesis. Wisz's (1999) finding that occupancy by martens of insular mountain ranges in Montana was well predicted by size of mountain range and distance to nearest other mountain range or the Rocky Mountain mainland is consistent with the equilibrium hypothesis. Wisz's (1999) findings therefore suggest that movements of martens between mountain ranges in post-glacial times may have been important

to the current distribution of martens in isolated mountain ranges. Pre-settlement martens in the Black Hills appear to have been ecologically isolated from the nearest naturally occurring populations in the Bighorn Mountains and Laramie Mountains. However, biogeographic evidence suggests that martens may have dispersed to other isolated mountain ranges east of the Rocky Mountains in post-glacial times (Wisz 1999), therefore the possibility of episodic colonizations or recolonizations of the Black Hills in the last 10,000 years cannot be precluded.

The apparently long distances between the Black Hills and the nearest marten populations to the west (Bighorn Mountains and, in pre-settlement times, Laramie Mountains) may be misleading, however, inasmuch as dispersal among these conifer forest islands likely has been via riparian forests and outlying pockets of conifers, which would shorten distances between major forests considerably (Figure 3). Thus, marten dispersal from the Bighorn or Laramie Mountains to the Black Hills in prehistoric times may have been facilitated by riparian forests, which could have reduced to nil the distances across non-forested habitats that martens would have to traverse, so that martens could move among mountain ranges at least over evolutionary time frames. On the other had, some evidence suggests that riparian forest on the western Great Plains at the time of settlement was not as extensive as today (Knopf and Scott 1990).

Distributional changes for the American marten across its range were summarized by Gibilisco (1994). The marten has been lost from most of the coast ranges of northern California (Kucera et al. 1995) and Oregon (Zielinski et al. 2001) since around 1950, from most of the Olympic Peninsula during the historical period (Marshall 1994), and from other large areas of Washington and Oregon. Martens have been lost from the southern part of their distribution in the central and eastern U.S., including Pennsylvania, Ohio and southern Wisconsin, but have reoccupied some of their vacated former range in Minnesota, northern Wisconsin and Michigan with afforestation. Martens also have recolonized southern New England, now being locally common in western Massachusetts. The only known changes in the distribution of martens in the Rocky Mountain region are their loss from the Black Hills and Laramie Mountains.

Figure 3. Coniferous and riparian forest vegetation of northeastern Wyoming, showing potential dispersal corridors between the Black Hills and marten populations in the Bighorn Mountains and Laramie Mountains.



Additional Information From Federal, State And Other Records

No information is available on the pre-settlement distribution of martens in the Black Hills. The last likely observation of a presumed native marten in the Black Hills took place about 16 km south-southeast of Lead on 26 August 1961 (South Dakota Department of Game, Fish and Parks 1996, unpublished). The reintroduction of martens to the Black Hills began in 1980-81, when 42 martens from Colorado were released (Fredrickson 1989, unpublished). Additionally, from 1990 to 1993 a further 83 martens were released in the central Black Hills (Fredrickson 1994, unpublished). Observations of animals, tracks and road-kills compiled by South Dakota Department of Game, Fish and Parks (1996) and by Fecske et al. (in review), show a roughly bimodal distribution of locations (sample size = 116) in the Black Hills, with the greatest concentration of observations in the northern part of the forest around Lead and Deadwood, and a smaller concentration of observations in the east-central part of the forest around the Norbeck Wildlife Preserve. Within the northern focus of occurrences, Spearfish Creek between Bridal Veil Falls and Chevenne Crossing has the highest concentration of records. Further information about the distribution of martens in the Black Hills is provided by track surveys in 1995-96 (Fredrickson 1996, unpublished), which produced 16 marten tracks: 10 in the Harney Peak area, two in the Dead Ox Creek area, two in the Galena area, and two in the Boy Scout Camp area.

The structural stages of the forest (Table 2, based on Buttrey and Gillam 1987) where these tracks were observed were stage 4 (mature, 13 records) and stage 5 (old growth, 3 records).

These records do not, in most cases, identify tree species dominants. Of the records in stage 4 (mature) stands, two were in 4a, seven in 4b, and four in 4c. Stage 4a stands are mature forest with <40% canopy closure, stage 4b stands are mature with 40-70% canopy cover, and stage 4c stands are mature with >70% canopy cover. Collectively these data provide some support for the hypothesis that martens in the Black Hills are selective of structural stage, tending to prefer mature and old-growth stands (Buttrey and Gillam 1987) dominated by white spruce (Picea glauca). They also are consistent with the hypothesis that martens occur in two foci in the forest. The distribution of martens in the Black Hills was shown by Fecske et al. (in review) to consist of a major focus in the area of Spearfish Canyon, extending southeast to near Custer Peak habitats in and near mature white spruce-dominated forest, and riparian zones, particularly at high elevations. Martens were least likely to occur in the Black Hills where forests were dominated by ponderosa pine (*Pinus ponderosa*) or deciduous species, trees were small in diameter, stands had <30% canopy cover, and stands were away from riparian zones. D. M. Fecske, (South Dakota State University, personal communication) has hypothesized that physical structure in the form of rock crevices and boulder fields in the Harney Peak area and elsewhere in the Black Hills may be important to martens.

Estimates Of Local Abundance

Marten populations and habitats are routinely managed in the absence of any estimate of relative or absolute abundance. Estimates of population size are available for only a few marten populations (e.g., Thompson and Colgan 1987), typically derived from research studies of small or island populations. The most common proxy for habitat quality and population density is home-range size, which is generally regarded as being inversely related to population density and habitat quality (Powell 1994). Home-range sizes of martens were reviewed and compared geographically by Buskirk and McDonald (1989), and varied, within a single study area in Ontario, from 1 km² for females in old forest with abundant prey to 11 km² for males in forest with extensive clearcuts 1-35 years old, with scarce prey (Thompson and Colgan 1987). No

estimates are available of population size, population density or home-range size for martens in the Black Hills. If information on home-range size were available, then a coarse measure of population density for martens might be inferred. If information on population size, recruitment, and survival were available, it would be possible to begin to parameterize a model of population persistence (population viability analysis, or PVA) for martens in the Black Hills.

Table 2. Structural stages of coniferous forest vegetation in the Black Hills, South Dakota and Wyoming, as used in this assessment, based on Buttrey and Gillam (1983). Specific attributes of structural stages are specific to a vegetation type (e.g. ponderosa pine).

Structural stage	Description	
2	Shrub-seedling. Seedlings are < 2.5 cm diameter at breast height (dbh)	
3b	Sapling-pole, canopy closures $40 - 70\%$	
3c	Sapling-pole, canopy closures >70%	
4b	Mature, canopy closures $40 - 70\%$	
4c	Mature, canopy closures >70%	
5	Old growth	

Population Trend

Year-to-year fluctuations in population size of the American marten are common, and typically correlated with fluctuations in densities of small mammals (Weckwerth and Hawley 1962, Fryxell et al. 1999). However, descriptions of long-term changes in densities are virtually absent from the literature. Our best indication of long-term trends in population size is on the basis of changes in distribution of the species (Gibilisco 1994, Kucera et al. 1995). Most of the range-wide population decline that has occurred in the last 150 years is likely due to local extinction and distributional losses, rather than to density declines in place. These changes in distribution are treated in the section on distributional dynamics. No estimates of population trend are available for martens in the Black Hills, although it is clear that martens were more abundant in 2000 than they were in 1980, before the reintroduction efforts. Whether the marten population has reached the carrying capacity of the habitat, is still growing, or is dwindling is likewise not known.

Population Viability

Required elements for a PVA have been reviewed by White (2000) and include a basic population model that includes a regulatory mechanism (density dependence), demographic stochasticity, temporal variation, variation among individuals, and, for long-term forecasting, genetic variation. For martens in the Black Hills, we currently have none of the above parameters, based on site-specific data. However, home range information combined with habitat occupancy would provide a coarse measure of population size.

Broad-Scale Movement Patterns

As described above, martens are believed to be behaviorally incapable of dispersing across non-forested habitats below the elevational limit of trees greater than 10-20 km. In contrast, martens commonly occur in non-forested areas above timberline in summer, using krumholtz conifers and talus boulders for overhead cover (reviewed by Buskirk and Ruggiero 1994). Therefore, conifer forest habitats separated by just a few kilometers of shrubland or grassland can be completely isolated from each other over ecologically meaningful time periods. This population insularity, in combination with small island size, leads to small, geographically closed populations, which are predisposed to stochastic and genetic processes that cause them to go extinct (Soulé 1987). Small mountain ranges isolated from the main Rocky Mountains are not likely to support viable populations of dispersal-sensitive, low-density forest-obligates for long periods (Table 3).

Table 3. Presence or absence of pre-settlement native marten populations in isolated mountain ranges east of the Rocky Mountain mainland, and approximate areas of coniferous forests in those mountain ranges.

Mountain Range	Area (Km2)	Presence Or Absence Of Martens
Black Hills	4971	Present
Little Belt Mountains	3874	Present
Big Belt Mountains	3499	Present
Bighorn Mountains	3445	Present
Laramie Mountains	2506	Present
Crazy Mountains	1639	Present
Bear's Paw Mountains	1320	Absent
Tobacco Root Mountains	955	Present
Pryor Mountains	823	Absent
Big Snowy Mountains	618	Absent
Highwood Mountains	538	Absent
Castle Mountains	433	Absent
Ruby Range	355	Absent
E. Butte Mountain	326	Absent
Bull Mountains	323	Absent
Little Rocky Mountains	222	Absent
Judith Range	157	Absent
W. Butte Mountain	114	Absent
North Moccasin Mountains	78	Absent
South Moccasin Mountains	53	Absent

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Areas are very approximate for some ranges because of outlying peninsulas and islands of coniferous forest. Areas for mountain ranges in Montana are from Wisz (1999), for the Bighorn Mountains and Laramie Mountains from Wyoming Gap Analysis of coniferous forest types, and for the Black Hills from Black Hills National Forest (1996a). Area of coniferous forest is an approximate predictor of the presence or absence of martens in isolated mountain ranges, with areas < 1000 km² generally lacking martens. The Black Hills is one of the largest isolated forest areas east of the Rocky Mountain mainland, although its area of moist coniferous forest likely is smaller than for some other isolated mountain ranges.

Although geographic variation in dispersal ability of martens doubtless occurs, it has not been described. Age-based variation in dispersal of martens has been described, in the sense that young animals, lacking territories, make up most dispersing or "transient" animals (Buskirk and Ruggiero 1994). Sexual differences in dispersal of fishers have been hypothesized (Williams et al. 2000) and inferred from population genetic studies (Aubry et al. in review); males tend to disperse farther than females, even as adults, presumably in search of mating opportunities. This leads to higher relatedness of females than of males from a site. If this pattern were true for martens as well as for fishers, I would expect that males would account for much of the broad-scale gene flow within the Black Hills, and between the Black Hills and nearby mountain ranges.

Habitat use at the mid-scale (several hundred meters) has been described for martens by three studies in the last few years. Chapin et al. (1998) in Maine, Hargis et al. (1999) in Utah, and Potvin et al. (2000) in Quebec examined selection at the scale of multiple home ranges. All three studies observed a fairly consistent upper limit to the amount of openings (including timber cuts and natural openings) in the forest tolerated by martens: 25-30% of a marten's home range. The cutting method on the site studied by Chapin et al. (1998) was clearcutting with 47% of the study area cut, but no sizes specified for individual cuts. Hargis et al. (1999) studied a series of 18 landscapes for which the mean proportion of area in clearcuts was 0.11 (range: 0-0.42), but clearcut size was not specified. The cutting method studied by Potvin et al. (2000) was the protection-of-regeneration technique, which used evenly spaced harvesting trails and left uncut strips 40-100 m wide, but clearcut size was again not specified. Potvin et al. (2000) showed a strong negative linear relationship (r = -0.78) between the size of the core area of the home range of martens and the proportion of it that was uncut forest (natural openings were very limited). Thus, martens increased the size of their home ranges as forest was cut, until their home ranges became too large to maintain, at which point the home range was abandoned and martens became locally extinct.

Within home ranges, martens have been shown consistently to avoid openings in the form of recent clearcuts (Koehler and Hornocker 1977, Soutiere 1979, Simon 1980, Spencer et al. 1983, Fager 1991), and this avoidance of openings is the basis of their strong mid-scale selection. The upper limit in the size of openings that martens have been observed to cross has varied from 10 m (Spencer et al. 1983) to 100 m (Koehler and Hornocker 1977). Buskirk (1983) described a marten crossing a 300-m wide unvegetated river bar in winter during a shift in home ranges. Rigorous studies of habitat use at this scale are scarce, but Robinson (1953) reported that martens in Colorado would travel no farther than 23 m from forest edges into meadows to reach baits in summer. The Black Hills National Forest Plan (1996a, I-19) specifies that the size of individual cutting units will be limited to 10 acres (4 ha), and refers to these as "patch clearcuts." Although I predict that martens avoid patch clearcuts in the Black Hills, it is unclear whether and to what extent martens avoid thinned ponderosa pine forests of the Black Hills. Post-release movements of translocated martens described by Fredrickson (1989) show that martens can traverse areas of

the Black Hills that include intensively managed ponderosa pine. Therefore, it appears that martens can move fairly long distances within the Black Hills.

An important factor in the isolation of montane islands of coniferous forest east of the Rocky Mountain mainland, including the Black Hills, is the potential importance of riparian forests in facilitating episodic movements. Whereas the straight-line distances from the Black Hills to the Bighorn Mountains, to the west, is about 160 km, riparian forest and small forest patches might reduce the distances across non-forested habitats that martens might need to traverse to only a few kilometers, or none at all (Figure 3). This is a plausible mechanism by which martens could have colonized or recolonized the Black Hills during the Holocene epoch.

Habitat Characteristics

General Considerations

In this section, I define habitat quality in terms of the fitness of animal occupants (Fretwell 1972). In the case of martens, fitness or components of fitness are difficult to estimate, even when compared to the difficulty for other mammals. Therefore, other attributes commonly are used as indicators of habitat quality, and I assume the validity of this substitution although it is largely untested (Buskirk and Powell 1994). The two most commonly used attributes from which habitat quality is inferred in research studies of martens are the behavioral choices of individuals and population density, for which home range size is sometimes used as a proxy. Behavioral choices of individuals should be reliable indicators of habitat quality, if martens recognize and prefer the best of a range of available habitats at some spatial scale (Buskirk and Powell 1994). Group selection has not been reported for any *Martes*, so using individual choices to reflect total fitness appears appropriate for American martens (Buskirk and Powell 1994). The use of population density to indicate habitat quality involves assumptions discussed by Van Horne (1983). The American marten appears to meet the criteria proposed by Van Horne (1983) for species in which population density is coupled to habitat quality: it is a habitat specialist, its reproductive rate is low, and it lacks a pattern of social dominance in high quality habitats, although there is evidence of avoidance by juveniles of high quality habitats occupied by territory-holding adults. Further, martens have not been reported to undergo seasonal shifts in home ranges (they have been shown to undergo seasonal contractions and expansions), and only rarely do they migrate in the face of environmental unpredictability. Therefore, the use of population density to estimate habitat quality seems valid and that validity is assumed here.

Habitat Selection By Martens In The West

In the West, martens tend to select for moist-site tree species that grow in stands characterized by living branches on the lower boles of trees, abundant coarse woody debris (CWD), and lengthy fire-return intervals. Martens will include other coniferous stand types in their home ranges, including dry-site species with few branches on the lower boles, sparse CWD, and frequent fire-return intervals, but select against them, in the sense of using them less than expected on the basis of availability. Importantly, apparent selection depends on the range of choices available, so that a stand type that is selected for (preferred) in one set of habitat choices will be selected against (avoided) in another (Raphael and Jones 1997). In the main Rocky Mountains, martens tend to select for stands dominated by moist-site species like Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), and select against stands dominated by drysite species with little physical structure near the ground, including most stands of ponderosa

pine and dry stands of lodgepole pine (*Pinus contorta*) (Buskirk et al. 1989, Buskirk and Ruggiero 1994). In the eastern Cascades, Raphael and Jones (1997) found martens using ponderosa pine stands with a bitterbrush (*Purshia tridentata*) understory. However, such an understory likely increases physical structure near the ground in ways not seen in ponderosa pine stands in the Black Hills. The scarcity and natural patchiness of mesic, spruce-dominated stands in the Black Hills mean that ponderosa pine in the vicinity of spruce-dominated stands likely is critical for habitat connectivity for martens. I predict that the value of ponderosa pine habitat to martens is a negative function of the distance of the ponderosa stand from a spruce stand large enough to attract martens.

Site moisture, fire-return interval, and physical structure are interrelated. Moist sites tend to have less frequent fire than dry sites, thereby encouraging the growth of species with fewer adaptations to fire, but good adaptations to shade in the understory (e.g., live branches and leaves on the lower bole). Also, the accumulation of CWD reflects long fire-return intervals, because large logs result from old trees. Structure near the ground fulfills the need by martens for protection from predators, access to subnivean spaces in winter, and protected resting sites (Buskirk and Ruggiero 1994).

Presumptive Marten Habitats In The Black Hills

Vegetative communities of the Black Hills have been described by Marriott et al. (1999, unpublished), and have ties to four North American biomes: Rocky Mountain Mainland Forest, Grassland, Eastern Deciduous Forest, and Northern Coniferous Forest, particularly the first of these. Ponderosa pine forest covers most of the Black Hills, and intergrades into ponderosa pine woodlands at lower elevations. Marriott et al. (1999:126) define woodland as, "Open stands of trees with crowns not usually touching (generally forming 25-60% cover)." Overall, ponderosa pine covers 84% of Black Hills National Forest (Black Hills National Forest 1996b, III-131). On moist sites (north-facing slopes and riparian zones) at higher elevations, especially in the northern part of the forest, white spruce stands are common; in many areas, these intergrade into ponderosa pine forest. White spruce – dominated habitats are rare forest-wide, composing only about 2% of the forest (Black Hills National Forest 1996b, III-131). Hardwood-dominated stands are common, and can be dominated by aspen (Populus tremuloides) and paper birch (Betula papyrifera) (which together cover 4% of the forest), bur oak (Quercus macrocarpa) and ironwood (Ostrya virginiana). Riparian shrublands at low elevations are dominated by mixtures of a wide range of species (Marriott et al. 1999, unpublished). Non-forested habitats, particularly grasslands, are common in the Black Hills, but are generally avoided by martens elsewhere in their range (exceptions include alpine zones [Buskirk and Ruggiero 1994], which are absent from the Black Hills), and are considered unsuitable habitats for martens and not treated further here.

Because it tends to develop little physical structure near the ground on frequently disturbed sites in the Rocky Mountains, ponderosa pine is generally considered poor or unsuitable habitat for martens (Buskirk and Ruggiero 1994). The main Rocky Mountains and isolated forest habitats east of the Rocky Mountain mainland other than the Black Hills (e.g., Bighorn Mountains, Crazy Mountains, Little Belt Mountains) feature a variety of moist-site conifers, including Engelmann spruce, blue spruce (*Picea pungens*), subalpine fir, and white fir (*Abies concolor*). But, the Black Hills lack all of these species, as well as Douglas fir (*Pseudotsuga menziesii*) (Little 1971), except where they have been introduced to a few sites. Thus, moist-site coniferous stands in the Black Hills tend to be dominated by a single species, white spruce, with admixtures of ponderosa pine and other dry-site species.

Fecske et al. (in review) conducted the only rigorous analyses of marten habitat selection at the landscape level for the Black Hills. They developed a model of selection based on track plates placed on 46 10.2-km²quadrats placed north of U.S. Highway 16 and east of the Wyoming state line. Placement of quadrats was based on a habitat relations model that predicted high quality habitat within the Black Hills. Their model, which predicted the probability of occurrence of martens on a site based on general knowledge of marten ecology, included dominant tree species (3 categories), tree diameters (3 categories), canopy cover (3 categories), distance to streams (2 categories), and elevation (2 categories). Predictions of the model were compared with 116 marten observations (1981-1995) collected by the South Dakota Department of Game, Fish and Parks. The model fit the observations well, showing that the attributes above predicted the occurrence of martens. Specifically, sites with white spruce as the tree dominant, large-diameter trees, high values of canopy cover, less than 100 m from a stream, and over 1585 m in elevation were most likely to have martens present. These findings are consistent with marten habitat associations elsewhere in the West.

The extent of habitats dominated by white spruce in the Black Hills is shown in Figure 4; most of this area is structural stages 3 and 4. Although spruce-dominated habitats are most common in the northern Black Hills, a band of spruce-dominated habitats extends northwest – southeast from around Deerfield to the Harney Peak area. The Bear Lodge Mountains, a peninsular extension of the Black Hills (about 2500 km² of coniferous forest) to the northwest, is contiguous with the main Black Hills by way of a corridor of ponderosa pine forest that extends southeast – northwest along Inyan Kara Creek. The Bear Lodge Mountains have no white spruce (Marriott et al. 1999, unpublished), therefore I hypothesize that the Bear Lodge Mountains hold no resident martens, and have habitat value for martens primarily as they may facilitate dispersal and colonization.

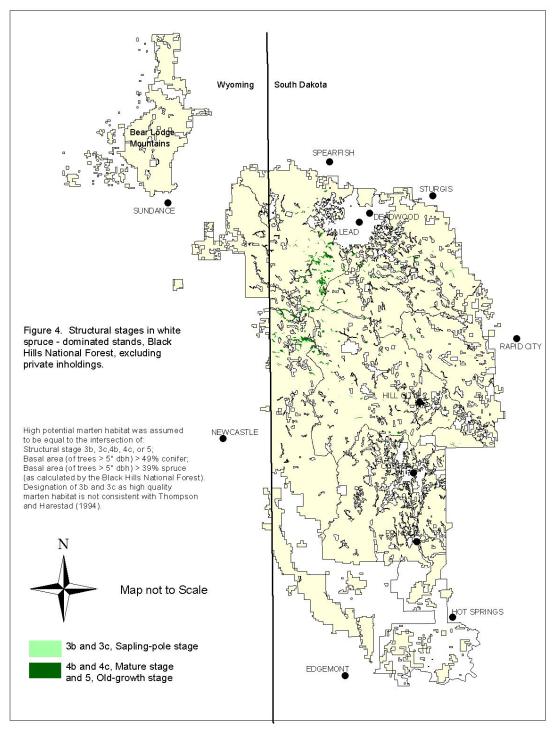
Because of the general association in the West of martens with moist-site conifers, which provide complex physical structure near the ground, in light of the findings of Fecske et al. (in review), and consistent with the few anecdotal data on marten occurrences in the Black Hills (Fredrickson 1996, unpublished; South Dakota Department of Game, Fish and Parks 1996, unpublished), I assume in this assessment that martens in the Black Hills select for and exhibit their highest survival and reproduction in stands dominated by mature or old-growth white spruce (structural stages 4b, 4c, and 5). This assumption is reflected in the mapping of presumptive marten habitat quality shown by Black Hills National Forest (1996b, Figure H-15), which assumes that only 7674 ha (1.2%) of the Black Hills National Forest is high-capability habitat for marten (structural stages 3, 4, and 5 are assumed suitable). Only about 225 ha of oldgrowth (stage 5) white spruce are mapped in the Resource Information System (RIS) data base (Black Hills National Forest 1996b, III-134). Habitat quality for martens elsewhere in the West and Fecske et al. (in review) tend to support the designation of structural stages 4 and 5 as high quality marten habitat (Black Hills National Forest 1996b), but it is doubtful whether structural stage 3 (sapling-pole) should be considered high quality marten habitat (Thompson and Harestad 1994). Whether or not structural stage 3 is considered high-quality habitat, the area of high quality marten habitat in the Black Hills National Forest is very limited relative to the size of the forest, and relative to the area likely needed for population viability for martens. I further hypothesize that mature or old-growth white spruce-dominated habitats serve as source habitats for martens that disperse to other, lower-quality habitats – particularly ponderosa pine stands – throughout the forest. A prediction deriving from this assumption is that mature to old-growth spruce stands should have older, territory-holding martens, whereas presumed lower quality habitats should hold younger, more transient animals. Another prediction resulting from this

assumption is that ponderosa pine stands near spruce stands will show higher use by martens than ponderosa pine stands far from spruce stands.

Although I assume that the habitat value of ponderosa pine to martens is low relative to moist forest types, the large area covered by ponderosa pine in Black Hills, in many areas interposing between white spruce – dominated stands, suggests that ponderosa pine habitats may be important for martens in the sense of connecting moist stand types. Indeed, it would be physically impossible for a marten to assemble a home range in the Black Hills without including some or a majority of ponderosa pine – dominated forest (Figure 4). Fecske et al. (in review) showed that having 6% of a quadrat in the highest quality habitat category and no more than 5% in low-quality habitat resulted in a 92% probability of martens being present. So, ponderosa pine forest near white spruce forest likely is important in stand connectivity and home range integrity in the Black Hills, and in predicting the presence of martens on a site, although it is not mapped as suitable habitat by the Black Hills National Forest.

Two important, generally opposing forces potentially affect the value of ponderosa pine as marten habitat in the Black Hills. The first is the tendency for ponderosa pine to regenerate in the absence of fire or other disturbance, so that ponderosa pine seedlings create structural complexity near the ground. Elsewhere in the West, ponderosa has tended to regenerate as a result of fire suppression, so that stands have an overstory of old trees and an understory of young ones (Everett et al. 1994). This regenerating understory could have habitat value to martens as cover, and help to connect spruce-dominated stands. The second, opposing force is the disturbance of ponderosa pine by patch clearcutting, thinning and fire. Little ponderosa pine in the Black Hills has not been affected by fire suppression, thinning, or timber harvest since pre-settlement times (Marriott et al. 1999, unpublished). To the extent that ponderosa pine in the Black Hills exhibits regeneration, with increased woody structure near the ground, how martens respond to this structure is unknown. On one hand, martens might capture small mammals associated with regenerating ponderosa pine and find the overhead cover suitable. However, regenerating ponderosa pine likely contains little CWD, or small mammals that are preferred by martens (see following section). Therefore, I predict that regenerating ponderosa pine is not high-quality habitat for martens, and is of primary value to martens during summer, and for movement among spruce-dominated stands. Although the relationships are unknown between disturbance and regeneration of ponderosa pine and habitat choices of martens in the Black Hills, they are potentially important for management of marten habitats, particularly where ponderosa pine is close to or connects spruce-dominated stands.

Figure 4. Structural stages in white spruce – dominated stands, Black Hills National Forest, excluding private inholdings in pocket Envirogram representing the web of linkages between American martens and the forest ecosystems in which they occur.



Food Habits

Diets of American martens, reviewed by Martin (1994) and Buskirk and Ruggiero (1994), vary seasonally and geographically. Martens eat a wider range of foods in summer than in winter, and in the southern part of their range than in the northern part. The most common foods are microtine rodents, particularly red-backed voles (*Clethrionomys* spp.), other voles (e.g., *Microtus* spp.), pine squirrels (*Tamiasciurus* spp.), flying squirrels (*Glaucomys* spp.), snowshoe hares (*Lepus americanus*), birds, insects, and berries.

Diets of martens in the Black Hills have not been studied. Of the species that are important foods for martens elsewhere, southern red-backed voles (*C. gapperi*), long-tailed voles (*M. longicaudus*), meadow voles (*M. pennsylvanicus*), red squirrels (*T. hudsonicus*) and northern flying squirrels (*G. sabrinus*) are found in the Black Hills. Snowshoe hares, which tend to be important foods of martens in the East (Martin 1994) are absent. Ground squirrels (*Spermophilus* spp.) and chipmunks (*Tamias* spp.) have been important foods of martens in a few studies, and deer mice (*Peromyscus maniculatus*) can be important but generally are not preferred. Based on marten diets elsewhere in their range, and lacking any studies of marten diets in the Black Hills, I assume that the important foods of martens in the Black Hills are southern red-backed voles, *Microtus* spp., northern flying squirrels and red squirrels. I predict that least chipmunks will have little importance to martens because of their occurrence in open habitats that martens tend to avoid, although they may be taken incidentally in summer.

Prey Species

Prey selection, meaning the comparison of prey used with prey available, has been analyzed in only a few studies. Although red-backed voles are the most important prey, other species are preferred even when red-backed voles are abundant. These preferred species include larger-bodied small mammals, typically of the genera *Microtus* and *Synaptomys*. Deer mice tend to be avoided in the sense that their apparent availability exceeds their use by martens, which may be due to the small body size of deer mice, to the habitats that tend to occupy, or to some behavior that tends to reduce their vulnerability to marten predation. Pine squirrels are relatively minor in marten diets, but increase in importance over winter and may be a substantive diet item in late winter and spring (Buskirk and Ruggiero 1994). Preference can be affected by microhabitats occupied by potential prey, by body size of prey, by taste or odors of prey, or by predator-avoidance behaviors of prey. No studies of prey preference by martens in the Black Hills have been conducted.

Characteristics Of Prey Species

Habitat associations of small mammals have been studied little in the Black Hills. Crompton (1994) described relative capture rates of southern red-backed voles, deer mice and least chipmunks in relation to timber management practices in ponderosa pine. However, he did not include white spruce, the presumptive preferred habitats of martens, in his study. Crompton (1994) was unable to discern statistical differences in habitat associations of small mammals, which have been readily shown to differ in their habitat associations in other studies (Hayes and Cross 1987). Crompton (1994) did not conduct power analyses to estimate the probability, given his sample sizes, of failing to detect selection, but such Type II errors must be suspected. Elsewhere, southern red-backed voles are associated with moist coniferous forest, particularly stands with abundant CWD (Nordyke and Buskirk 1991), although they occur in mixed stands that include ponderosa pine in Idaho (Hayward and Hayward 1995). Size of logs on the forest

floor has been shown to be particularly important, either because red-backed voles feed on ectomycorrhizal fungi found in older coniferous stands where large logs are common, or because they need large logs for cover. I hypothesize that southern red-backed voles in the Black Hills are primarily associated with moist forest stands dominated by white spruce, and are particularly associated with dense CWD in structural stages 4-5.

Red squirrels in the Rocky Mountains are associated with cone-bearing ages of conifers, particularly lodgepole pine (Finley 1969) and spruce (Sullivan and Moses 1986). North of the geographic range of Abert's squirrel (*Sciurus aberti*), red squirrels occur in ponderosa pine and feed on ponderosa pine cones (Ferner 1974), and I assume that ponderosa pine is important, although perhaps secondary, red squirrel habitat in the Black Hills. Red squirrel middens have been shown to be important for resting by martens in winter (Buskirk 1984), but whether this relationship is important in the Black Hills is not known.

Flying squirrels tend to associate with white spruce in the Black Hills, being most common in the moist canyons in the northern part of the forest (Turner 1974). *Microtus* tend to occur in association with herbaceous understory or herbaceous meadows.

Breeding Biology

Phenology Of Courtship And Breeding

The phenology of courtship and breeding of American martens has been reviewed by Mead (1994): martens mate from late June to early August, undergo 6-7 months of embryonic diapause, and give birth in April and May. No information about courtship and breeding of martens in the Black Hills is available.

Courtship Characteristics

Martens exhibit a brief courtship followed by vigorous and sometimes prolonged copulation (Henry and Raphael 1989). No information on courtship by martens in the Black Hills is available.

Natal And Maternal Den Site Characteristics

Natal and maternal dens of American martens have been reviewed by Ruggiero et al. (1998) and Schumacher (1999). Martens tend to give birth in stands with high densities and diameters of snags and CWD, and in association with red squirrel middens. Natal dens tend to be in tree boles above the forest floor, whereas maternal dens tend to be closer to the forest floor. No information is available on natal or maternal dens of martens in the Black Hills, but den sites could represent an important habitat need of martens.

Litter Size

Litter size of American martens has been reviewed by Mead (1994) and mean litter sizes range from 2.7 – 3.0 (Ashbrook and Hanson 1927, Markley and Bassett 1942, Wright 1963). Pregnancy rates are lower and litter sizes smaller in yearling than older females (Strickland et al. 1982). Litter sizes are smaller than predicted on the basis of body size (Buskirk and Ruggiero 1994); martens are not prolific producers of young. No information is available on pregnancy rates or litter sizes of martens in the Black Hills.

Parental Care

In American martens, male parental investment in reproduction is limited to copulation. Maternal care includes lactation, defending the young, moving them among den sites, and bringing food to them (Buskirk and Ruggiero 1994). No information is available on parental care in martens in the Black Hills.

Site Fidelity

Site fidelity relates to the tendency to disperse and to establish and confine movements to home ranges. Martens tend to disperse out of parental home ranges at ages that depend on study area; no consistent age or season of dispersal has been reported (Buskirk and Ruggiero 1994). Females tend to establish home ranges and restrict their movements to them. Male martens, like other polygynous mustelids, tend to establish home ranges larger than predicted on the basis of body size, and make forays beyond their home range boundaries during the mating season (Powell 1994). Beyond a post-release movement of one marten described by Fredrickson (1989, unpublished), no information on site fidelity of martens in the Black Hills is available.

Demography

Demography of American martens has been described primarily for trapped populations (e.g., Strickland and Douglas 1987, Thompson and Colgan 1987); sex and age structure and vital rates of untrapped populations are poorly understood (Powell 1994). A particular problem with studies of trapped populations is that trapped animals are usually assumed to be representative of the population, which may not be true. Powell (1994) provided estimates of age structures of various marten populations under varying harvest regimes. No information is available about demography of martens in the Black Hills.

Life History Characteristics

Life history characteristics of American martens have been described by Buskirk and Powell (1994), and Buskirk and Ruggiero (1994). The American marten has a K-style life history strategy, with high longevity and small litter sizes. Martens live as long as 14 years in the wild (Strickland and Douglas 1987), an exceptional age for their small body size, but the average life expectancy of neonates likely is measured in months rather than years. For females, age at first breeding is generally 1 year, with first litters produced at 2 years of age. Pregnancy rates varied with age; about 80% of yearling females and 93% of older females conceived (Strickland and Douglas 1987). Mean litter size was 3.0 across all age classes. The conservative K-style strategy of martens suggests that martens cannot respond quickly to dramatic population declines or environmental changes, an important consideration in their conservation. No information is available on life history characteristics of martens in the Black Hills.

Survival And Reproduction

Survival of martens has been described for trapped (e.g., Hodgman et al. 1994) and untrapped (e.g., Hodgman et al. 1997) populations. In an untrapped area, Hodgman et al. (1997) found that survival was higher for adult males (annual rate = 0.87) than adult females (annual rate = 0.53), whereas in an intensively trapped area, the opposite was the case (adult male survival for 1 May - 15 December = 0.12, adult females = 0.39). Overall \ddot{e} (population size at a later time/population size at an earlier time) for the intensively trapped population was 0.57, which indicates that the site was a pronounced population sink, and that the observed mortality rate was

not sustainable (Hodgman et al. 1994).

The best information on ecological influences on reproduction comes from Thompson and Colgan (1987), who showed that during a period of food shortage in Ontario, martens experienced delayed reproductive maturity and reduced ovulation rates. No information is available on survival and reproduction of martens in the Black Hills.

Social Pattern For Spacing

Powell (1994) discussed population structure and spacing patterns for martens and fishers. He showed that population size of *Martes* can fluctuate by a factor of more than 10 in response to fluctuations in prey populations. Weckwerth and Hawley (1962) documented a 4-fold change in population density of American martens over a 5-year period, and Thompson and Colgan (1987) reported a 6-fold change in response to prey populations. Home ranges are the basis of population organization in all *Martes*, and some evidence suggests that the size of home ranges is negatively correlated with resource abundance (Buskirk and McDonald 1989, Powell 1994). However, many other factors (method of depicting boundaries, sample sizes, sex, residency status, season) confound comparisons of home-range sizes, so that effects of resource availability may not be apparent in small samples.

Home ranges of adult martens tend to be territorial within sexes (Powell 1994), the entire home range is a territory, and marked geographic variation in home range size has been shown by Buskirk and McDonald (1989). Martens are not territorial between sexes, and tolerate the presence of juveniles of both sexes. The smallest reported home ranges of American martens (< 100 ha) have been those from near Glacier National Park (Burnett 1981), and the largest ones from a high-elevation area of southern Wyoming (> 1400 ha, O'Doherty et al. 1997). No defense of den sites has been reported, although aggression toward conspecifics and smaller carnivores doubtless occurs. Fredrickson (1989, unpublished) showed home range polygons of translocated animals in the Black Hills, but the residency status of the animals, sample sizes and method of depicting home ranges were not described. No other information on home range sizes of martens in the Black Hills is available.

Local Density Estimates

Density estimates for American martens are derived from attempts at exhaustive trapping and marking or from telemetry, and have been reviewed by Buskirk and Ruggiero (1994). Estimated densities have ranged from 0.4/km² in clearcut forest (Soutiere 1979) to 2.4/km² in uncut forest during a year of prey abundance (Thompson and Colgan 1987). No estimates are available of densities of martens in the Black Hills.

Limiting Factors

Presumed limiting factors for martens are represented by an envirogram (Figure 5). An envirogram is a currency-free representation of proximal and more distant factors believed to affect the distribution and abundance of a species (Andrewartha and Birch 1984, Van Horne and Wiens 1991). The relative importance of these factors is not represented.

The marked avoidance of most non-forested habitats by martens suggests that overhead cover is a primary limiting factor, both in a distributional sense and in the placement and differential use of home ranges. Within home ranges, physical structure near the ground is the most important limiting factor to martens, with CWD being the most valuable form of structure both for prey

habitat and potential resting and denning sites. Others factors (e.g., snow, lower branches of live trees) can also contribute to structure near the ground. Ruggiero et al. (1998) proposed that dens and resting sites could limit the distribution and abundance of martens.

Metapopulation Structure

As stated above, some biogeographical evidence (Wisz 1999) suggests that insular and mainland marten populations in Montana are in colonization-extinction equilibrium, suggesting Holocene movements of martens among isolated habitats and the Rocky Mountain mainland. If so, the marten populations of the Rocky Mountains could be functioning as a core-satellite metapopulation, with the main Rocky Mountains functioning as the core. As a core – satellite metapopulation, the core population and some isolated populations east of the main Rocky Mountains would contribute to dispersal to and recolonization of even more isolated populations, but the more isolated populations would contribute little or nothing to the viability of the core population. Thus, I hypothesize that under natural Holocene conditions and over millennia, the Bighorn and Laramie Mountains contributed to recolonization of the Black Hills marten population after episodic extinctions, but contributed little to the marten population in the Rocky Mountain "core."

The current distribution of martens within the Black Hills suggests two foci of occurrences, one in the moist, white spruce – dominated stands of the northern Black Hills south of Spearfish, and one around Harney Peak. The Harney Peak area also features some white spruce, which tends to be uncut because of protection provided by the Norbeck Wildlife Preserve and Black Elk Wilderness area. Further, the Harney Peak area features large boulders and rock outcrops, which could be important structure for martens. Observations of martens also occur along a rough line between these foci, so that movements between these areas may occur by way of a habitat corridor. These two foci likely are too close together to be considered a metapopulation, but movements of martens between the two areas might be important to the persistence of one or both. If one of the population units were much smaller than the other, then the smaller one would be more likely to depend on dispersive movements for its persistence. However, I emphasize that, aside from released animals, and recognizing that telemetry studies of martens are underway, no information is available on marten movements within the Black Hills.

Community Ecology

Predators

Predation here is considered killing for food (Taylor 1984). Predation on martens has been noted anecdotally in a number of studies reviewed by Strickland et al. (1982), most commonly by coyotes (*Canis latrans*), fishers, bobcats (*Lynx rufus*), and lynx. Some studies (e.g. Hodgman et al. 1997) do not distinguish between predation and other kinds of killing, but the pooled effect of these two kinds of mortality can be large: 8 of 15 deaths observed by Hodgman et al. (1997), and 18 of 22 deaths observed by Bull and Heater (2001). When martens are killed but not eaten by other vertebrates, it is properly considered interference competition or interspecific strife, considered below. The effects of trapping on marten populations are considered separately, below.

Competitors

Competition here is considered the "... negative effects which one organism has upon another

by consuming, or controlling access to, a resource that is limited in availability" (Keddy 1989). Two kinds of interspecific competition are recognized: exploitation competition, in which one competitor gains access to a resource before another, and interference competition, in which one competitor denies another access to the resource through aggressive behavior, including killing. Exploitation competition among carnivores has been difficult to demonstrate in field studies, but interference competition is increasingly recognized as a powerful influence on community structure of carnivores (Buskirk 1999, Buskirk et al. 2000), including American martens. Larger-bodied species tend to win these competitive interactions, and the interactions are most likely between species that are similar in body size. Interspecific killing (as well as predation) of martens by avian or mammalian predators has been important in some studies; Bull and Heater (2001) found that 18 of 22 martens that died in their Oregon study area were killed by avian or mammalian predators. Bobcats were the most important single cause of marten deaths, killing eight animals.

Other insights into interspecific interactions involving martens are provided by zoogeographic data; Krohn et al. (1995, 1997) have shown that the sympatry of the American marten and fisher is mediated by an abiotic factor, snow. Fishers are larger than and competitively dominant to martens in areas with shallow or crusted snow, but fishers cannot persist in areas with deep, soft snow, to which martens are well adapted (Krohn et al. 1995, 1997). Fishers do not occur in the Black Hills, but the same principle could apply to marten interactions with coyotes or bobcats, the most likely competitive interactions of concern for martens in the Black Hills. The mediation of hypothesized competition between martens and other mammalian predators by snow can be further affected by human over-snow travel, which compacts the snow surface and has been hypothesized to provide covotes with avenues into areas with deep, soft snow that they otherwise could not reach (Buskirk et al. 2000). This hypothesized human facilitation of access to deepsnow areas by mammalian predators could increase competitive losses by martens, with population-level implications. Black Hills National Forest is a particularly likely site for these hypothesized interactions, because road densities are the highest of any national forest in the region (2.37 mi/mi₂ [1.47 km/km₂], Baker and Knight 2000), and winter recreation, including snowmobile use, is extensive and not limited to the road system. It is difficult to predict how road type affects this relationship, but roads that receive enough vehicle use to maintain trails in snow are likely more important than those that receive so little vehicle use that snow is soft and uncompacted most of the winter. For unpaved roads that have some regeneration and no off-road vehicle use, the facilitation of competition with martens likely is minimal. So, although competition with or predation on martens by other carnivore species has not been shown in the Black Hills, I hypothesize that it is an important mortality source for martens, and is mediated by snow characteristics, as modified by human over-snow travel. Bobcats are common in the Black Hills (Turner 1974, Higgins et al. 2000). Red foxes (Vulpes fulva) are of the right body size to be potential interference competitors with martens, and occur in a few areas of the Black Hills (Higgins et al. 2000), so red foxes must also be considered potential competitors with martens in the Black Hills. I emphasize that no information about competition with martens in the Black Hills is available.

Parasites, Disease, And Mutualistic Interactions

A wide range of helminth, protozoan, and arthropod parasites has been described for American martens (e.g., Poole et al. 1983). Reported infectious diseases of American martens include sylvatic plague (Zielinski 1984) and canine distemper (Fredrickson 1990). No information is available specific to the Black Hills about parasites, diseases, or mutualistic interactions

involving martens.

Trapping

Fur trapping has been an important economic and recreational value of American martens historically, and remains so in some areas today (Todd and Boggess 1987). Trapping of martens is permitted in some states (e.g., Wyoming, Montana), but not others (e.g., Colorado, Utah; see Table 1). Potential future trapping was an important justification for the reintroduction of martens to the Black Hills (Fredrickson 1980, unpublished), but marten trapping is not allowed in the Black Hills today. The management of trapped marten populations was a major emphasis of marten biology in the late 1970's and early 1980's, when pelt prices were high (Strickland et al. 1982). Since then, pelt prices have declined, and fur trapping and marten trapping have become less common and less important economically.

Depending on various factors, trapping can have diverse effects on marten populations. In areas with high quality habitat, where trappers hold exclusive, long-term rights to the area trapped, and where there is adequate regulatory infrastructure, trapping can be sustainable and provide recreation and income (Strickland and Douglas 1987). However, where habitats are poor, trappers are transient or compete for pelts on the same trap-line, and regulatory mechanisms are lacking, trapping can quickly over-harvest marten populations (Strickland 1994, Fortin and Cantin 1994). Martens are easily caught by inexperienced trappers (Strickland et al. 1982). In an intensively trapped area in Maine, Hodgman et al. (1994) found that trapping caused 90% of total mortality, and inferred that this high rate was not sustainable and was exacerbated by a road system that facilitated access for trappers, and extensive timber harvesting (46% of area had received timber harvest). Hodgman et al. (1994) also concluded that because 93% of total trapping mortality occurred during the first 14 days of the season, shortening the season to 2 weeks would be an ineffective means of limiting trapping mortality.

Regulatory mechanisms used to assure that trapping does not over-harvest marten populations include licensing, setting season lengths and dates, setting harvest limits, assigning trappers exclusive rights to trapping areas, establishing refugia, and selective trapping of species or sexes. Each of these approaches has been discussed by Strickland (1994). Assigning trappers exclusive rights to geographic areas creates incentives to harvest sustainably. Selective trapping involves the use of live traps to enable the trapper to examine the animal before deciding whether to harvest it, and allows selective harvest of some species or sexes. In a system of refugial management, some areas are protected from harvest, and martens outside refuges may be trapped without limit (Buskirk 1994). This method does not require estimates of population size or trend, or setting or enforcing harvest limits. However, it does assume some properties of the refugia and trapped areas. First, it assumes that refugia are established in areas with habitat quality high enough to produce a net outflow of dispersing animals ($\ddot{e} > 1$); if refugia are established in lowquality habitat and high-quality habitat is intensively trapped, a population could be driven to extinction quickly. Further, it assumes that mortality in trapped areas is not 100%; some animals should migrate from trapped areas back to refugia and reproduce (Morris 1991). Lastly, the refugium concept tacitly assumes that the spatial arrangement of refugia and trapped areas is such that refugial sub-populations have good persistence properties collectively (Buskirk 1994). A refugial management system in which the refugia are too small to hold subpopulations with significant persistence through time could be a formula for population extinction.

Marten trapping in the Black Hills was carried out for many decades by European people, although we have no information about trapping patterns, numbers of martens harvested, or the

population-level effects of trapping. We also lack information on the extent to which trapping contributed to the apparent extinction of the native marten population. Marten trapping has not been allowed since the reintroduction of martens in the 1980's. A PVA would allow the quantitative examination of factors likely to affect the marten population in the Black Hills, and should be undertaken before reaching a decision as to whether to resume trapping. The effects of a possible trapping program on martens would be a function of several factors:

Population Size

We have no estimates of population size in Black Hills, therefore it is impossible to estimate how many martens could be harvested. The larger the population, the larger the number of animals that could be harvested sustainably. If estimates of home-range size and habitat occupancy (area of land filled with marten home ranges) were available, it might be possible to estimate population size in a coarse way, but that information is not available currently.

Habitat Quality

Although we have no estimates of habitat quality for martens in the Black Hills, the preponderance of ponderosa pine forest, the intensive management of that forest, and the presumed low value of managed ponderosa pine forest to martens cause me to hypothesize that most of the marten habitat in the Black Hills is lower quality than mainland Rocky Mountain forests dominated by moist coniferous forest. No evidence suggests that martens can attain high densities in areas dominated by intensively managed ponderosa pine. This assumed low habitat quality, combined with the small area of the Black Hills as a whole, suggests that the number of martens that can be sustainably harvested from the Black Hills is small.

Other Mortality Sources

Trapping mortality cannot be viewed as a stand-alone factor in marten population management, but must be considered in the context of population productivity and the full range of human-caused mortality. In wilderness areas, trapping might be the only substantive human-caused mortality source, but the Black Hills is heavily used for recreation (Black Hills National Forest 1996b, III-417), is intensively roaded (Baker and Knight 2000), has little statutory wilderness (3930 ha or 0.8% of the land area, Black Hills National Forest 1996b, III-409), and has many private inholdings (Black Hills National Forest 1996b) where martens can die of human causes. Therefore, I hypothesize that martens in the Black Hills have higher rates of death from non-trapping human causes than those in areas with more wilderness character. These causes can include vehicle collisions, shootings, non-target captures in traps set for other species, killing by dogs, disease transmitted by domestic species, and ingestion of toxins at human habitations or around vehicles. If non-trapping human-caused mortality of martens is high, the number of martens that can be removed by trapping can be expected to be correspondingly low.

Regulatory Mechanisms

Marten trapping can be regulated to assure that over-harvesting does not occur. Such regulations can include the establishment of refuges in high-quality habitats, assignment of trappers to exclusive areas for multiple years, setting of harvest limits, or requirement of selective trapping, using live traps (Strickland 1994). A trapping program meeting these specific conditions could benefit marten conservation by providing information on marten populations; it could require the submission of marten carcasses, which could be the source of information about demography,

vital rates, and diseases, for which we now have no information specific to the Black Hills.

Other Complex Interactions

Many of the ecological relationships affecting martens are doubtless complex, however, we have no information on such complex interactions for martens in the Black Hills.

Risk Factors

The most important threats to the viability of martens in the Black Hills include poorly regulated trapping, intensive timber harvest in certain habitats, and the stochastic processes that result from small population size. Poorly-regulated trapping of martens, in high quality habitats, by trappers competing with each other seems capable of threatening the Black Hills marten population, given the extensive motorized access to virtually every area the size of a marten's home range within the forest.

Intensive harvesting of timber from the presumed best-quality habitats, those dominated by white spruce, seems capable of reducing the carrying capacity of the Black Hills for martens to a level below population viability. The important elements of intensive harvesting in these stand types are reductions in canopy cover, removal of CWD, loss of future recruitment of CWD, reductions in size of future CWD, and increases in road densities. Each of these factors has been shown to affect habitat use, habitat preference, or habitat quality for American martens. This prediction assumes that the Black Hills is a small, ecologically isolated population, that martens in the Black Hills are highly dependent on white spruce for population persistence, and that intensive harvesting along the lines I have described in white spruce – dominated stands would reduce habitat quality for many decades. The processes that affect small isolated populations include stochastic events, inbreeding and genetic drift; the marten population in the Black Hills could be susceptible to these without negative effects from trapping or habitat loss.

Several other factors that could affect the viability of the marten population in the Black Hills vary in their plausibility. Further, their likely effects on marten would depend on interactions among them. They include changes in densities of paved roads or intensity of use by off-road vehicles, the occurrence of catastrophic fires in large areas of white-spruce forest, the translocation of fishers or other competitors of martens to the Black Hills, and the outbreak of a disease, such as canine distemper, that has high virulence to martens (Fredrickson 1990). Roads can have a range of effects on martens, including killing them as a result of collisions, causing martens to avoid areas near active roads (Robitaille and Aubry 2000), facilitating human collection of fuel woods near roads, and increasing exposure of martens to pets and human foods.

Marten Responses To Habitat Changes

Management Activities

Timber Harvest

Timber harvest has been hypothesized to have variable effects on martens, depending on cutting intensity. Thompson and Harestad (1994, Figure 26.3) predicted two different relationships between percentage of forest that was removed by cutting and relative carrying capacity, depending on cut patch size. For clearcutting (cut size > 3 ha), they predicted a linear decline in

carrying capacity, with a 50% loss of carrying capacity at about 50% forest "removal." For dispersed removal (patch cutting), they predicted an increase of carrying capacity by about 25% with a 25% forest "removal," then a decline in carrying capacity with further cutting. This prediction was based on the assumption that martens move short distances into recently cut areas to exploit resources there, but cannot travel into the centers of large clearcuts. Since then, three studies of landscape-scale habitat use (Chapin et al. 1998, Hargis et al. 1999, Potvin et al. 2000) have examined the relationship of fragmentation to marten density for clearcutting and found that martens are far more sensitive than predicted by Thompson and Harestad (1994, see discussion above). An evaluation of the marten habitat in the Black Hills relative to the thresholds reported by Chapin et al. (1998), Hargis et al. (1999), and Potvin et al. (2000) would be very useful in forecasting the likely effect of future timber harvesting activities on martens, but would require identifying the habitats considered by these authors to be "non-forest" or "deforested."

The studies just described were conducted in forest types of likely higher quality, and Thompson and Harestad (1994) assumed a forested matrix of higher habitat quality for martens than apparently occurs in the Black Hills. Dry-site ponderosa pine far from any white spruce may have so little habitat value for martens that its management has few implications for carrying capacity for martens, other than providing dispersal corridors. Also, patch cutting or patch clearcutting of ponderosa pine at intensities predicted by Thompson and Harestad (1994) to benefit martens may not improve carrying capacity for martens in the Black Hills, as a result of a lack of any positive response of martens to any resources in recently cut ponderosa pine. The resolution of this question would require information on how food and cover resources for martens respond to thinning or patch clearcutting of ponderosa pine. I predict that habitat value for martens resulting from patch clearcutting of ponderosa pine on dry sites would decrease from low to nil; this prediction assumes that as a result of patch clearcutting of ponderosa pine, martens would no longer travel through stands that they formerly could traverse.

The effects of timber harvesting in white spruce forest on martens would depend on structural features over the successional sequence. Early and mid-successional stages of white spruce – dominated stands may have more physical structure and more berry-producing shrubs than the same stages in ponderosa stands, making them correspondingly better habitats for martens. However, the appropriate frame of comparison would seem to be the uncut stand, and no evidence currently shows that carrying capacity for martens can be increased by timber harvest in any pattern, at any scale.

Recreation

Responses of martens to changes in recreation management regimes have not been studied, nor have predictions been posed as to how martens should respond to various kinds or intensities of recreation. The most plausible hypothesized effects of recreation on marten in the Black Hills are through increased deaths caused by vehicle collisions, and via facilitated access of coyotes to snowy areas as a result of intensive snowmobile use. This assumes widespread dispersed recreation in winter. In addition, increased numbers of forest users associated with dispersed recreational use could cause a wide range of negative effects on martens, including shooting, killing by dogs accompanying recreationists, or providing access to toxins. Off-road vehicles are potentially important as they facilitate dispersed recreation, impeded vegetative recovery on abandoned roads, and compact snow, facilitating movements by competitors of martens. I am not aware of any plausible means by which recreation could affect marten populations positively.

Livestock Grazing

Marten habitats have not been studied relative to livestock grazing, and livestock grazing in forests has not been hypothesized to be an important influence on marten habitats. Clearly, the effects of livestock grazing on martens would depend on the species of livestock and the specific grazing practices. If forests were clearcut or patch to encourage forage for livestock, particularly if such cleared areas were near riparian spruce-dominated forests, the effects on martens would be negative and could be severe. Martens make virtually no use of grasslands or shrublands except at forest edges, therefore livestock grazing in extensive grassland or shrubland habitats are predicted to have few or no implications for marten habitat quality or population viability. Livestock grazing in forested areas could affect martens by altering physical structure near the ground and standing crops of herbaceous plants, the latter of which could affect small mammal abundance. If livestock grazing strongly influenced moisture regimes, including water tables in riparian zones, the distribution of mesic forest types, specifically white spruce, could be affected, with strong implications for marten habitats. Inasmuch as CWD is likely too heavy to be moved or trampled by livestock, I assume that this important habitat component for martens would not be affected by livestock. It is plausible that livestock grazing could affect marten populations positively if it stimulated the growth of herbaceous plants in forested settings, which in turn stimulated increased densities of small mammals.

Mining

Mining embraces a wide range of activities, with widely varying effects on vegetation, water quality, and behaviors of animals (e.g., Phillips and Lipton 1995). Surface mining can be expected to have a much greater effect on vegetation and therefore on habitat quality for martens than sub-surface mining, because of the larger area of land presumably affected by surface mining. Mining can result in road construction, which has implications for marten populations because of loss of forested area, and increases in traffic – related deaths. The production of metal leachates as a by-product of ore refining, and the seepage or discharge of metal leachates to surface waters could increase concentrations in vegetation (Saiki et al. 1995) or aquatic organisms (Poulton et al. 1995) to levels that cause tissue lesions. These effects have been found to be important at the population level for various semi-aquatic mammals (Blus and Henny 1990) and terrestrial birds (Larison et al. 2000). Larison et al. (2000) showed that the White-tailed Ptarmigan (Lagopus mutus) in the Colorado Rockies contained high and toxic levels of cadmium, that concentrations increased with age, and that ptarmigan were less dense within a belt of high cadmium concentrations near the surface than outside the belt. White-tailed Ptarmigan were vulnerable to metals contamination because they fed on willows (Salix spp.), and willows tend to bioconcentrate metals. Larison et al. (2000) expected that cadmium loads would be higher at lower elevations, as a result of metals released into surface and shallow ground water by mining activities, and their results were consistent with this hypothesis. Martens in the Black Hills have not been shown to be closely linked to aquatic food sources, therefore I predict that effects of mine-produced leachates on martens are low. However, if martens in the Black Hills were found to eat foods with close ties to aquatic systems or riparian willows, this hypothesis could be rejected. I am unaware of any plausible means by which mining could affect marten populations positively.

Prescribed Fire

I assume here that prescribed fire would tend to be used in areas that had evolved in association with fire and under conditions that would not be likely to lead to high intensity crown fires,

particularly in white spruce forest types. Specifically, I assume that prescribed fire would tend to be used in ponderosa pine forest, grasslands, or shrublands, and that white spruce would neither be targeted for prescribed burns, nor strongly affected by prescribed burns because of its relatively mesic character. However, prescribed burns that burned out of control could invalidate these assumptions. I predict that prescribed fire in shrublands and grasslands would have little effect on habitat for martens, although stimulation of herbaceous plants by fire could cause increased population densities of small mammals that could disperse into forests, or could be accessible to martens near forest edges.

Prescribed fire has implications for martens where it is set in forests. General effects of fire on forest vegetation are described in the FEIS for the Forest Plan (Black Hills National Forest 1996b, III-211). I assume that southern red-backed voles and red squirrels are important prey of martens, and that neither of these species would be positively affected by fire. However, wildfire has been shown to improve habitat quality for martens in Alaska and Yukon, at least in the shortterm (Vernam 1987), where high densities of CWD are recruited to the forest floor, succession favors high densities of herbaceous plants in early successional stages, and small mammals respond positively to early post-fire successional stages. Where mature trees are killed and overstory canopy removed by prescribed fire, and post-fire successional stages do not generate a lot of physical structure near the ground, I predict that the loss of overstory canopy will reduce the ability of martens to traverse the area. This prediction is based on the assumption that a canopy layer of ponderosa pine addresses the "psychological need" (Hawley and Newby 1957) of martens for overstory cover. Therefore, the effect of prescribed fire on marten habitat should depend on the value of the habitat to martens before the fire, on fire characteristics, on whether overstory-producing trees are killed, and on post-fire successional trajectories. Fires in dry ponderosa pine forests with no white spruce habitats nearby would have a low probability of affecting martens, because the habitats are likely to have little value to martens before the fire. Fires in ponderosa pine forest near or connecting white spruce stands are predicted to affect marten habitats negatively by reducing woody structure near the ground. However, I recognize that prescribed fire might be a necessary alternative to other kinds of disturbance, particularly wildfire, and that wildfire has been a natural feature of the environment of the Black Hills over evolutionary time spans. Therefore, it is reasonable to hypothesize that although martens may not preferentially use habitats in the Black Hills that have evolved with frequent fires and that are likely to be targeted for prescribed fire, martens have evolved with fire in a general sense, and should not be adversely affected by fires, prescribed or wild, over long time intervals.

Fire Suppression

Fire suppression includes actions intended to prevent and extinguish fires. Fire suppression should, at least in the short term, be beneficial to martens because it produces longer fire-return intervals, more continuous vertical and horizontal distribution of fine woody materials (Black Hills National Forest 1996b, III-211), and increased densities of CWD, particularly that < 8 cm in diameter. In the long term, fire suppression can lead to increased need for alternative forms of disturbance, including thinning and prescribed fire, and to higher likelihood of high-intensity fires. Thus, the effects of fire suppression on martens represent a trade-off over short vs. long time intervals. In the short term, fire suppression increases the probability that white spruce and habitats nearby will retain large amounts of woody structure near the ground. In the long term, fire suppression increases the probability of catastrophic fires that could cause major losses to spruce-dominated habitats, presumptive key habitats of martens.

Non-Native Plant Establishment And Control

Introduced plant species for the Bear Lodge portion of the Black Hills were described by Marriott (1985). A more complete list of introduced plant species is not known. The effect of introduced plants on martens is not known.

Fuelwood Harvest

I assume that fuel wood harvest includes removal of live trees, snags and CWD, and that snags and CWD removed for fuel wood would be mostly in early decay classes (classes 1-2, ref), meaning that they were not highly decomposed. Martens (Corn and Raphael 1992) and redbacked voles (Hayes and Cross 1987, Tallmon and Mills 1994) have been shown to associate closely with CWD; therefore, fuel wood harvest has the potential to negatively affect marten habitats. The effect of fuel wood harvest on martens likely will depend on several factors, such as volume and diameter of fuel wood removed, and habitat value for martens before fuel wood removal. Large-diameter CWD has been shown to be important to red-backed voles; therefore, small diameter CWD may be less important to this species. Based on these factors, harvest of large volumes of large-diameter CWD from late-successional stands dominated by white spruce within the presumed foci of marten occurrence in the Black Hills is predicted to affect martens more negatively than harvest of small volumes of small-diameter CWD from dry midsuccessional stands of ponderosa pine far from areas of marten occurrence. Typically, fuel wood collection occurs near roads, so areas near roads in the Black Hills are the most likely candidates for fuel wood collection. Restriction or removal of roads in spruce-dominated areas should be considered as a means of minimizing the effects of fuel wood collection on martens and their prey.

Natural Disturbance

Insect Outbreaks

Insect outbreaks are potentially important to martens because they can cause the deaths of large numbers of trees, thereby altering stand age and physical structure, initiating stand replacement, and abruptly recruiting large numbers of snags or volumes of CWD. Outbreaks of insects are important in disturbance regimes of coniferous forests in the West (Veblen 2000). In some parts of the Northeast, martens have been found to prefer forests 30-50 years after outbreaks of spruce budworm (Choristoneura fumiferana), because of the complex physical structure near the ground contributed by insect-killed trees, and rapid regeneration of some conifers (Potvin et al. 2000). Of course, the effects of catastrophic tree death are confounded by whether the stand is salvaged; Hargis et al. (1999) observed negative landscape-scale habitat effects on martens associated with stands killed by mountain pine beetle (*Dendroctonus ponderosae*), but these stands had been salvaged. It was not clear whether the deaths of trees or the removal of boles caused the negative response of martens. In general, and in the absence of salvaging, insect outbreaks that cause massive tree death can be expected to reduce habitat quality for martens in the short-term, by removing overstory canopy. For the mid- and long term, effects on martens of insect outbreaks in the Black Hills should depend on sizes and proportions of trees killed, rates at which the tree boles are recruited to positions near the ground (sooner should be better), and rates of regeneration. Those effects could be negative or positive; no information is available on the effect of insect outbreaks on marten habitats in the Black Hills.

Wildfire

Wildfire can have a wide range of potential effects on martens in the Black Hills, depending on size and intensity of fire, stand type, fire frequency, and post-fire successional trajectory. Some of these potential effects are described under "Prescribed Fire." I assume that wildfire will have a wider range of effects than prescribed fire, because prescribed fires generally are set under a narrower range of weather and stand conditions. The effects of wildfire on martens have been studied in Yellowstone (Fager 1991), northern Idaho (Koehler and Hornocker 1977), and interior Alaska (Vernam 1987). In Yellowstone, martens made almost no use of the recent (1988) burns, although martens passed through burns and rested on unburned islands (Fager 1991). In Idaho, martens were found to be favored by a mosaic of burned (60 years before) and unburned moist stands (Koehler and Hornocker 1977), where the burned area composed about half of the study area, and varied in fire intensity. Koehler and Hornocker (1977) also noted that dry forest types were suitable only for deer mice, not preferred foods of martens, especially just following fire. In Alaska, martens attained high local densities in post-fire successional stages that had abundant CWD and herbaceous vegetation (Vernam 1987). In this case, CWD was contributed by rapid recruitment of burned boles to the forest floor. However, the positive response of martens to post-fire successional stages generally is limited to Alaska and northern Canada. So, although martens respond positively to post-fire early successional stages in some, particularly moist settings, I predict that the general response of martens to post-fire successional stages in the Black Hills will be negative. I predict that martens in the Black Hills will be affected strongly and negatively by intensive, large fires in white spruce stands, but affected little by small, lowintensity fires in dry ponderosa pine. I hypothesized above that fires in shrublands would not affect martens appreciably, because martens do not venture far into shrublands, however, if shrubs were replaced by herbs following fire, then martens in forests near such sites could benefit from higher densities of small mammals responding to herbaceous vegetation. The same could be true of grasslands, which martens also avoid. Again, I note that martens have evolved with fire in the broad sense of the term, although they tend not to prefer forest types, particularly dry-site types, with a history of frequent fires.

Wind Events

Wind, especially tornados and microbursts, is capable of altering the physical structure of forests very quickly, killing large numbers of trees, and recruiting boles to positions near the ground (Veblen et al. 1989). Such wind events have not been studied in relation to marten habitats, but they could resemble those of insect outbreaks; catastrophic tree death occurs, CWD increases abruptly, canopy cover decreases abruptly, but forest floor vegetation is mostly undisturbed. No information is available on the effect of wind events on martens in the Black Hills or elsewhere.

Other Weather Events

Other weather events potentially important to martens include freezing rains and unusually heavy snowfalls. Martens have evolved in close association with snow, and should be benefited by deep, soft snow. The effects of freezing rain on martens is difficult to predict, and has not been reported in the literature.

SUMMARY

Populations of the American marten are apparently stable over much of its western North

American range, but a conservation concern in a few western jurisdictions. Trapping of the marten for fur, common throughout its western range 60 years ago, has become restricted or banned in several states. The marten is an indicator species or planning tool for a large number of forested jurisdictions in the West, including most national forests in which the marten occurs.

The marten has a K-style life-history strategy, with small litters, high longevity, and large spatial requirements for its body size and trophic level. Therefore, marten populations should be unable to respond quickly to sudden environmental changes or mortality events. Populations are structured around intrasexual territories, and home range size is generally considered to be a crude index of habitat quality or resource density, with large home ranges indicating scarce resources.

Martens in western temperate North America occur in coniferous forests and habitats nearby, and select for moist stands with complex physical structure near the ground. These stands tend to be late successional stages, although martens travel through other habitat types and include a wide range of habitat types in their home ranges. The basis of the association of martens with structurally complex forests is related to their needs for avoiding their own predators, accessing prey beneath the snow, and finding protected microenvironments for resting in winter and giving birth and sheltering neonates.

The Black Hills are depauperate of moist coniferous forests and species typical of moist forests. The predominant conifer in the Black Hills is ponderosa pine, with small areas of white spruce – dominated forest that are potentially key to the viability of the Black Hills marten population. Ponderosa pine should be low in habitat value to martens, although some evidence shows that martens can travel through ponderosa pine forest, and it is clear that martens in the Black Hills must incorporate ponderosa pine-dominated stands into their home ranges. Landscape configuration of ponderosa pine and white spruce stand types in the Black Hills should be important to martens.

Diets of martens are more diverse in summer than winter, and include primarily vertebrate prey, especially red-backed voles, other microtine rodents, tree squirrels, flying squirrels, and snowshoe hares. Of these, all but the last species are present in the Black Hills. So, although habitats for martens in the Black Hills are somewhat atypical, the usual prey base is mostly present. Red-backed voles and flying squirrels should be most common in white spruce forests; the distribution of red squirrels and other likely prey across stand types is not known.

Martens in the Black Hills may exhibit population structure at two scales. The Black Hills may have been part of a metapopulation that included the Rocky Mountain mainland, Bighorn Mountains, or Laramie Mountains in pre-settlement times. Weak anecdotal evidence suggests the existence of some population subdivision within the Black Hills, with foci of marten occurrences in the northern Black Hills and around the Norbeck Wildlife Preserve. At both scales, the existence of metapopulation dynamics could be important for population viability of martens in the Black Hills.

The factors most likely to be limiting to martens in the Black Hills are extensive cutting of white spruce forests, fuel wood cutting in or near spruce-dominated stands, high-intensity fires over large areas of spruce-dominated forest, and weakly regulated trapping. Some evidence suggests that white spruce is important to martens in the Black Hills, and extensive conversion of late successional white spruce to early successional stages could have negative population-level effects on the species. The effect of cutting, thinning, and prescribed burning of ponderosa pine on marten populations should depend on type of treatment and on proximity to white spruce, and

therefore to likely home ranges of martens. The effect of trapping on martens should depend on population size, habitat productivity, number of animals trapped, other kinds of mortality experienced by the marten population, and regulatory measures employed.

The effects of recreation on martens are not known, but widespread use of over-snow vehicles in winter may facilitate access by coyotes and other generalist predators to marten home ranges, causing increased competitive interactions in which martens are losers. Livestock grazing is predicted to not have important effects on martens. The effects of mining on martens should depend on the form and extent of mining. Prescribed fire and wildfire are likely to have impacts in proportion to the extent to which they occur in marten home ranges. High intensity fire in vast areas of white spruce forest should affect martens negatively, but low intensity fire in ponderosa pine away from spruce stands should affect martens little or not at all. In general, martens have evolved in association with fire over most of their western distribution. Major disturbance events, including wind events and insect epidemics, have the potential to kill large numbers of trees, and recruit large volumes of CWD to the forest floor quickly. Martens are likely to be negatively affected by such events in the short term, although, again, they have evolved with these forces in western coniferous forests. Martens have not evolved in association with natural disturbance events in combination with large-scale removal of tree boles, as occurs through timber harvest.

REVIEW OF CONSERVATION PRACTICES

Management Practices

Management practices used for martens in North America include protection in conservation reserves (e.g., state and national parks), bans on trapping (Forsey et al. 1995), regulated trapping (see section above), and timber management prescriptions that consider needs of marten populations (Watt et al. 1996). Ontario has made the most intensive use of the marten as a forest planning tool (Watt et al. 1996), and has established guidelines at landscape and stand levels. However, the guidelines may not be applicable to the Black Hills due to differences in ecological conditions

Management practices available to managers to benefit the marten population in the Black Hills are limited. Based on currently available information, it appears that the maintenance of the area of spruce-dominated stands, and maintenance of structural stage, diameter class of tree boles, and diameters and volumes of CWD near the expected natural range, tending toward late structural stages, large boles, and large diameters and volumes of CWD would be affect the marten population in the Black Hills most positively. Further, it appears that the protection of sprucedominated stands from fragmentation processes such as increases in edge, or perforation with small cuts or roads, would retain existing habitat value for martens. Maintaining high canopy cover in stands adjacent to spruce-dominated stands also appears to be important for allowing habitat connectivity for martens. The value of structure to martens near the ground in such stands is not yet known. Where stands near spruce-dominated stands are thinned, the retention of boles in arrangements that might provide cover for martens could be an important mitigating measure for martens. It may be necessary to provide replacement stands for white spruce affected by stand-replacing fires; late-stage spruce-dominated stands may not be present in perpetuity, and replacements may require management action. Grazing and other land uses may have important consequences for the retention or restoration of the mesic character of riparian sites, with

important implications for spruce-dominated stands. The sustainability of trapping for martens can be evaluated with a PVA, which can show what levels can be expected to be harvested sustainably, and to what factors persistence is especially sensitive.

Models

Models of potential use in conserving martens include those for habitats and those for populations. Allen (1984) modeled habitats for martens using 4 predictor variables (V_i), as follows:

V₁: Percent tree canopy closure. This suitability index assumes that sites with less than 25% tree canopy cover have zero value to martens, a linear increase in suitability to optimal at 50% canopy closure, and optimal habitat value >50% canopy closure.

V2: Percent of overstory canopy closure composed of fir or spruce. This suitability index assumes that overstory with zero spruce or fir component has a habitat suitability of 10% of optimal, a linear increase in suitability to optimal at 40% spruce or fir, and optimal habitat value at >40% overstory being spruce or fir. Although the model assumes that Douglas fir has value equal to that of other fir species, this assumption was based on results in Idaho, where Douglas fir occupies much moister sites than in the southern Rockies.

V₃: Successional stage of stand. This suitability index assumes that shrub – seedling stages have zero habitat value, and a linear increase in habitat value through pole – sapling and young stages. Optimal habitat value is only found in mature or old-growth stages. Support for this assumption was provided by Thompson and Harestad (1994), who showed that martens do not show preference, in the sense of use exceeding availability, until stands reach "mature" or "overmature" stages.

V4: Percent of ground surface covered by downfall >7.6 cm in diameter. This suitability index recognizes the general importance of CWD. However, it assumes that sites with 0% of the ground covered by CWD >7.6 cm in diameter have 50% of optimal habitat value, increasing linearly to optimal habitat value at 20% of the ground covered with CWD, optimal habitat value at 20-50% of the ground covered with CWD, and linearly decreasing habitat value from 50% of the ground covered with CWD to 100% (50% of optimum habitat value). It is most unlikely that CWD only 7.6 cm in diameter has value to martens for predator avoidance or thermoregulation, and it is also unlikely that having 20% of the ground covered with such small-diameter material would be optimal for martens, as V4 suggests. The mean diameter of CWD used by martens for resting in southern Wyoming was 39 cm (Wilbert et al. 2000); this value provides a more realistic regionally based estimate of the size of CWD useful to martens. In southeast Alaska, mean diameter of logs used by martens for resting was 87 cm (Schumacher 1999).

The suitability indices are combined through multiplication and taking the square root of the product, so that a zero value for any suitability index renders the overall habitat suitability index zero.

Bennett and Samson (1984b, unpublished) modified the Allen (1984) model slightly for application to the central Rocky Mountains. Lacking data for marten habitat use in the Rockies, Bennett and Samson acknowledged the hypothetical and untested nature of their model. Other habitat models for martens have been developed for the Sub-Boreal Spruce zone of Canada (Lofroth and Banci 1991, unpublished), California (Barrett and Spencer (1982, unpublished), and

Maine (Ritter 1985, unpublished). Testing or validation of habitat suitability models for martens has been undertaken only by Barrett and Spencer (1982, unpublished), who found a significant, but not particularly strong correlation between model predictions and habitats used by martens. Schneider (1997) developed a spatially explicit model of marten habitat for western Newfoundland that predicted the distribution of martens 75 years into the future. The habitat suitability model for the fisher in the Great Lakes region was tested and found to be strongly predictive by Thomasma et al. (1991).

Survey And Inventory Approaches (Presence - Absence)

Methods for surveying the presence-absence of forest carnivores, including martens, have undergone considerable development in the last decade (Bull et al. 1992, Zielinski and Kucera 1995). The primary methods for monitoring include remote cameras, track plates, and snow tracking. The first two of these methods involve baiting. The relative merits of these three approaches were compared by Zielinski and Kucera (1995, Table 1-1). Cameras can be used at any season, detect multiple species, and require moderate training and relatively little labor, but involve high initial costs in the purchase of remote cameras. Track plates are useful primarily in summer, detect a smaller range of species, require little training and moderate labor, and require little cost in materials. Snow tracking is useful only in winter, detects multiple species, and requires intensive training and a lot of labor, but has very low cost for materials. Each of these methods has some potential utility in the Black Hills, depending on the goal of the survey and funding levels available.

Monitoring Approaches (Habitat, Population Trend, Presence - Absence, And Persistence)

Habitat monitoring is best undertaken in a Geographic Information System setting, and assumes knowledge of high-quality habitats for martens. A logical and feasible objective of habitat monitoring would be to determine, over a period of decades, trends in area, shape, and size of spruce-dominated stands. A second objective of habitat monitoring could be to determine, over a period of decades, the structural characteristics of spruce-dominated stands and stands nearby. These characteristics could include tree sizes, understory characteristics, and volumes and diameters of CWD. Monitoring of presence – absence of martens is best accomplished with one of the methods described above (Survey and inventory approaches), and would be the basis of inferences about persistence of marten populations through time. In particular, it is important to understand the distribution of martens relative to spruce-dominated stands. If martens, through time, extend their distribution to areas far from spruce stands, the implications for marten populations and habitat management are large. Population trend can be inferred from changes in numbers of occurrences at track-plate stations (Zielinski and Stauffer 1996) or other detection sites. Zielinski and Stauffer (1996) modeled the sample sizes needed to detect 20% and 50% declines, with 80% power (20% probability of not detecting a change of the specified magnitude that had actually occurred), in the proportion of track stations that detected martens. To detect a 20% decline, they estimated that 115 stations within a stratum (a subset of the population of stations created on the basis of preliminary sampling) would be needed. To detect a 50% decline, only 17 stations per stratum would be needed. Other methods based on telemetry or markrecapture would provide more reliable estimates, but the cost would be prohibitive outside of a research setting. For the Black Hills, after an initial survey of the distribution of martens, periodic (5 - 10-year) track plate surveys using strata identified from preliminary sampling

would provide statistical evidence (estimates of the probabilities of not detecting a difference when there is a difference from Zielinski and Stauffer [1996]) of changes in the distribution of martens among sites. Although not a true estimate of relative abundance, it would estimate habitat occupancy, which should be a rough surrogate for population size, assuming that home range sizes of martens did not vary with population density. The frequency of such surveys would represent a trade-off between cost and continuity; surveys conducted too infrequently could suffer from variation in methods between surveys.

ADDITIONAL INFORMATION NEEDS

Additional information needed to support the development of scientifically sound, forest-scale conservation of the marten in the Black Hills is summarized in Table 4. Distribution is the highest priority because it would provide spatially explicit information on the parts of the forest that martens currently occupy and, by inference, that need to be managed specifically for martens. Broad-scale correlations of marten occurrences with stand types from these distributional data would provide information on habitat use and selection by martens. Stand-scale habitat selection by martens is a high priority because the hypothesized association of martens with white spruce – dominated stands is a key assumption of much of this assessment.

Stand-scale studies of habitat selection, most plausibly based on telemetry data, would also provide information on preferred structural stages, movements between stands, and home range sizes. Cause of mortality is an intermediate-priority information need because human-caused mortality must be suspected as an important factor in a setting as strongly influenced by humans as the Black Hills. Such a study, likely also based on telemetry, could also provide information on mortality rates, which could be used to parameterize a model of population persistence (population viability analysis). Landscape-scale habitat associations are considered intermediate in importance because this information would be the basis for designing landscapes that will support viable populations of martens. Estimates of population size usually are not available in managing populations of martens, but the geographic closure of the Black Hills population facilitates and increases the importance of such an estimate. Population size is a central piece of information in a population viability analysis, and could be estimated by various means, including mark-re-observation based on marking of animals, or on micro-satellite DNA markers that can be amplified from hairs collected at baited hair snares. Vital rates (age-specific birth rates and death rates) are essential if a full population viability analysis of the Black Hills marten population is to be completed.

Table 4. Additional information needed to support the development of scientifically sound, forest-scale conservation of the marten in the Black Hills, South Dakota and Wyoming. If various objectives were addressed in a multifaceted study, estimated costs would be only partially additive.

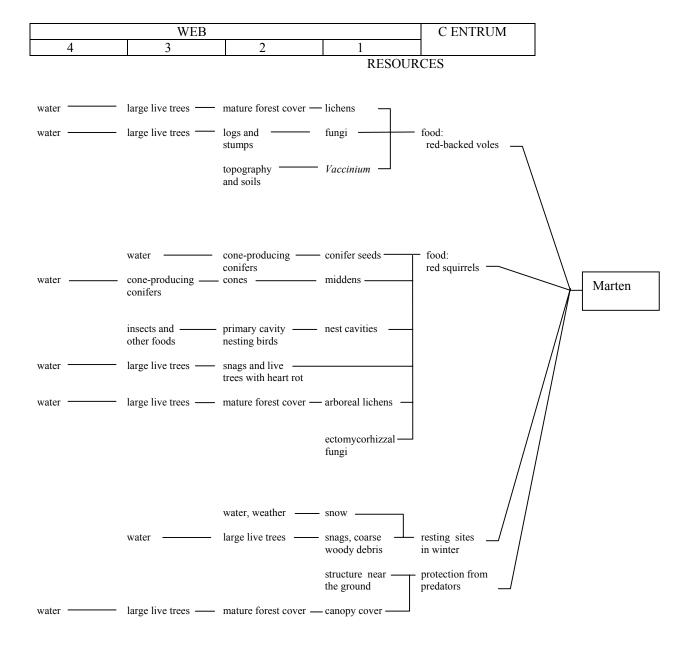
Subject	Priority*	Justification	Cost**
Distribution	High	Understand the extent of the forest occupied by	Low
		martens	

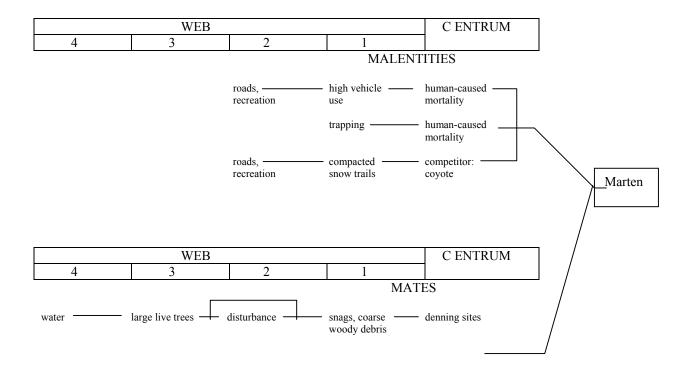
Stand scale habitat associations	High	Understand stand attributes that promote survival and reproduction of martens	Intermediate
Causes of mortality and vital rates	Intermediate	Estimate survival rates and causes of death to set management strategies that will minimize human-caused deaths. Parameterize a model of population persistence (population viability analysis).	High
Landscape scale habitat associations	Intermediate	Understand landscape configurations that contribute to survival and reproduction of martens	Intermediate
Population size	Intermediate	Estimate population size to better understand population biology and parameterize a model of population persistence (population viability analysis)	Intermediate

^{*} Low: would refine or improve marten management strategy; Intermediate: would be required for management of populations or habitats with a high likelihood of success; High: is necessary for any science-based management strategy

^{**} Low: estimated cost = \$1000-10,000; Intermediate: estimated cost = \$10,000-100,000; High: estimated cost = \$100,000-250,000

Figure 5. Envirogram representing the web of linkages between American martens and the forest ecosystem in which they occur. Predation on martens is understood too poorly to represent, but competition with martens is shown in malentities.





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DEFINITIONS

- Carrying capacity the ability, expressed as density, of an area of land or water to support a particular kind of organism, reflecting habitat, predators, prey, and competitors.
- Conspecifics individuals of the same species.
- Dispersal movement by organisms, particularly juveniles, to areas away from their sites of birth.
- Ectomycorrhizal plant root systems infected with a fungus in what is often a beneficial relationship (the fungus assists the plant with mineral absorption).
- Embryonic diapause suspension of the embryonic development of an animal at the stage of the blastocyst, which floats free in the lumen of the uterus for several days to many months, after which it imbeds in the uterine wall and resumes development.
- Fitness the differential representation of genotypes through generations. The sum of all the factors that affect this differential representation, especially survival and reproduction.
- Krumholtz dwarf, wind-sculpted conifers at timberline.
- K-style life history a life history strategy based on high longevity, long periods to sexual maturity, and low reproductive output.
- Polygynous a mating system characterized by some males mating with multiple females.
- Refugia areas where animals are not trapped, and where habitat is protected from human-impacts.
- Stochastic random, not predictable except in probabilistic terms.
- Subnivean beneath the snow.
- Sympatry (of two taxa) occurring together, having overlapping geographic ranges.
- Taiga northernmost boreal forest and woodland, typically characterized by coniferous trees with crowns that do not touch, and small tree sizes.
- Taxon species or other level of biological organization (e.g. subspecies, genus, family)

Uncertainty – inability to predict the behavior of a system.

Woodland - open stands of trees with crowns not usually touching (generally forming 25-60% cover)